CONCERNING "FAIRY RINGS" IN PASTURES

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(With 1 Text-figure.)

In the year 1911 I published the results of an investigation of two fairy-ring-forming fungi(1) which are commonly met with in pastures—*Marasmius oreades* (Fr.), the fairy-ring champignon, and *Clytocybe gigantea* (Sow.). I have since observed other fairy rings, caused by fleshy fungi, in order to compare their growth with those already studied, which have ceased to exist.

In 1922 Professor Buller called my attention to the work of Shanz and Piemeisel on the "Fungus Fairy Rings of Eastern Colorado" and their effect on vegetation(5). These authors, in addition to their own investigations, give an exhaustive epitome of the work that had hitherto been published on fairy-ring fungi, referring to notes or investigations by 31 authors in connection with 47 fleshy fungi. Since the observations and conclusions of these authors, especially with regard to the cause of the death of the vegetation, do not always agree with mine and those of other investigators, a short review and criticism of the subject of "fairy rings" may not be without interest.

Shanz and Piemeisel distinguish three types of fairy rings in Eastern Colorado—I have noted the same three types in England.

They are:

Type I, those in which the grass is killed or badly damaged;
Type II, those in which the grass is only stimulated;
Type III, those which produce no effect upon the grass.

Type I. This is perhaps the most interesting and the one which has been investigated most frequently, as it appears on lawns, bowling greens and golf courses, or in pastures. *Marasmius oreades* (Fr.) is a good example in England of this kind, but according to Shanz and Piemeisel not in America. Such rings may often be met with in poor pastures, where about June the full effect of the presence of the fungus on grass may be seen.

Three zones (Fig. 1) may be noted to such rings:

(*a*) an inner zone where the grass is deeper green and much more luxuriant than the grass within the ring, and that of the pasture generally,

(*b*) surrounding this, a zone of dying or dead grass, and

(*c*) a narrow outer zone of stimulated grass situated externally to (*b*). This outer zone gradually broadens until about towards the end of September it may be even broader than zone (*a*).

A sod of the middle zone is well permeated with fungus hyphae to the depth of about one foot, visible even to the naked eye, and dense wefts of fine white hyphae cling round dying roots, and when atmospheric conditions are very humid mass on the surface of the soil. Under high magnification the fungus mycelium can be seen penetrating the roots of the grass, the soft parenchymatous cortical parts of which it entirely consumes.

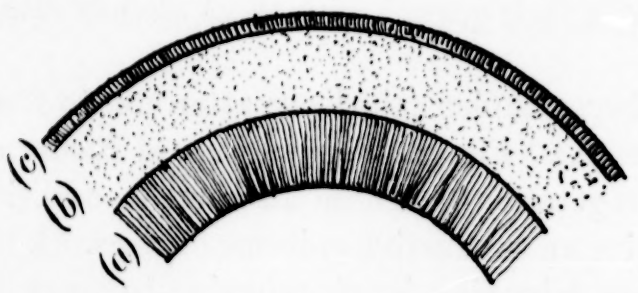

Fig. 1. Diagram showing the different zones of a fairy ring, caused by *M. oreades*. (*a*) Inner dark green grass zone. (*b*) Dead grass zone. (*c*) Outer dark green grass zone.

A curious physical phenomenon is also to be noted in this zone, that is, the resistance offered to the percolation of water; hence the soil of this zone is always dry compared with that of the zones on either side or in the field generally. This I have proved elsewhere(1) to be due to the air entangled within the meshes of the mycelial network occupying the spaces between the particles of soil. On this zone the sporophores of the fungi appear, usually on the inner side of it, but frequently in other parts, about a month after the dying down of the grass.

In a sod of zone (*a*)—the innermost zone—the mycelium is present in far less quantity than in the middle zone, being scarcely visible to the naked eye and in an impoverished and dying condition. The luxuriance of the grass growing on this zone appears to be due to the fertilising qualities of the decomposition products produced partly by the fungus in destroying the plants (grass and others) of this area and partly as the result of the decomposition of the mycelium itself.

The rich dark green appearance of the grass on the outer narrow

zone (*c*) is due to the stimulating action of the fungus when it begins its attack on the grass, for as with many other parasites stimulation of growth is often the first effect of the parasite on the host. The amount of mycelium on this zone at first is not great and although rootlets are continually being destroyed there is evidence(1) that more are rapidly formed. No doubt the grass is further stimulated by the saprophytic action of the fungus rendering available the products of decomposition of any dead rootlets occurring among the living plants of the sod.

During late autumn and winter these fairy rings are scarcely visible, for the dead grass zone recovers its vegetation: owing to the penetration of neighbouring rhizomes and to the germination of seeds.

Hence in a fairy ring of *type I* we see a regular annual progress of a parasitic fungus living on grass in the soil and gradually proceeding outwards, fairly uniformly in all directions from the centre, where it started, presumably from the germination of a spore. As it advances it destroys the roots of the grass and finally after killing the plants consumes all the softer tissues. The mycelium now being without food and having rendered this area unsuitable for further growth by the secretion of toxic (staling) substances, produces sporophores and then dies. The soil of this zone is thus much enriched and when a new growth of grass appears, it shows a luxuriant growth. Meanwhile hyphae continue to grow forward, attack a new zone and the same sequence of events is repeated. The sequence extends over three years; in the first year the grass is being attacked, in the second it succumbs to the attack, in the third year a new crop of grass benefits from decomposition products rendered available by the mycelium which killed the preceding crop of grass and also from the decay of the mycelium itself.

Clytocybe gigantea (Sow.) is another fungus which must be included in *type I*: these rings usually appear three or four weeks later than those of *M. oreades*; they do not fruit every year, nor is their fruiting season so prolonged as the former. The dead grass zone does not recover its vegetation so quickly; one that I observed for three years(1) showed the bare zone for a whole year instead of two or three months—the period usual in the case of *M. oreades* rings.

It seems highly probable too that the rings of *Tricholoma gambosum* (St George's mushroom) belong to *type I*, since a zone of dead grass usually appears in connection with these rings.

Shanz and Piemeisel have paid most attention to the rings formed by *Agaricus tabularis* (Peck) (a fungus allied to *A. arvensis*) which also belongs to *type I*. The only point of difference between these American

rings of *A. tabularis* and the English *M. oreades* is in the position of the sporophores which are said to come up on the outer stimulated zone instead of as in the case of the English *M. oreades* anywhere on the bare zone.

A very curious feature to be noted in connection with the fairy rings of Eastern Colorado is that *M. oreades* does not behave like *type I* there: it does not do any damage to the grass and therefore in America must be classed as *type II*. All investigators of *type I* agree that these rings are associated with poor pastures and discouraged by high nitrogenous manuring.

Much discussion has arisen as to the cause of the outward progression. Why does the fungus progress as a ring not as a disc? Why does it never grow backward and attack the grass again in the centre of the ring?

In my researches of 1909–11 I have shown that the fungus excretes something toxic to itself (staling substances(1)). The presence of this together with the exhaustion of the nutrient material in the soil would account for the fungus growing outward into a more favourable zone, and would also account for the dying out at the point of intersection of two meeting rings. The fact that these rings are usually found in poor pastures also has some bearing on this point. I have proved in the case of both *M. oreades* and *Clytocybe gigantea* that if the grass in front of an advancing ring is manured with ordinary stable manure the rings die out; if manured only in patches the rings die out in patches. Doubtless in poor pastures the grass being of feeble growth falls an easy victim to the parasitic fungus, but when stimulated to active growth by nitrogenous manure it resists the onslaught of the parasite. The fungus never grows backward into the zone it has left because it would first have to encounter certain staling substances, which bar the way, and even if these were not there, the now very vigorous plants occupying this zone are not likely to yield easily to the attack of a parasite.

Most investigators have drawn attention to the fact that the soil of the middle zone of a fairy ring, especially during late spring and summer, always contains relatively less moisture than the zones on either side and also than the soil of the field generally, and several, including Ritzen Bros.(5) (1901) and Molliard(4) (1910), attribute the death of the vegetation to this dry condition of the soil. Shanz and Piemeisel also consider this the cause of the death of the vegetation noted in the rings formed by *A. tabularis*—the fungus hyphae prevent the percolation of rain water and the intense drought produced leads to the death of the vegetation: these authors consider that no harmful effect could be noted

in these rings so long as the soil contained available water. This is quite contrary to my observations in the case of *M. oreades* rings. As I have already stated, I attribute the death of the vegetation to parasitism on the part of the fungus, a conclusion to which Ballion has also arrived.

In my researches of 1909–11 various experiments (1) pointed to the presence of a toxic excretion produced by the fungus which damaged the roots of the grass and enabled the fungus to attack them even before they were dead. Since reading the work of Shanz and Piemeisel (5) I have repeated my investigation of the soil in connection with the fairy rings caused by *M. oreades* and I confirm my statement that among the roots of the grass plants on the outer edge of the outer dark green zone the first attack of the fungus mycelium on the rootlets can be seen and that it is indicated by a brownish discoloration of the delicate root tips or of the external cortical tissue near this region, and by loss of symmetry of the root hairs. Very little mycelium is present and as this increases discoloration becomes more pronounced, and I would emphasise that this is at a time when the moisture content of the soil is practically normal, for it is seen on the advancing edge of the ring. If plants just behind this area be examined during January and February when the moisture content of a fairy ring is much the same as that of the field generally, and compared with plants taken from normal turf, no difference will be apparent except at the roots when it will be seen that these when washed free from soil, look rusty coloured because of the numerous dead and dying rootlets.

There is evidence that the fungus is producing a toxic effect upon the young rootlets. In experiments where uninfected roots have been left 24 hours in very damp infected soil, the rootlets turn brown or black: in a control experiment using uninfected soil, the root tips remained unchanged and uninjured: the toxin seems to be injured by heat, since the effect is far less pronounced when the soil is sterilised first. Young roots also turn black when allowed to remain 24 hours in an extract of infected soil from which all soil and fungus mycelium have been filtered off. In the controls of boiled extracts or of extract from uninfected soil the roots remained uninjured. Infected roots, besides having the rusty appearance, always show more copious branching which points to an effort on the part of plants to make up for the destruction of root apices which is constantly going on.

Since in this outer infected zone, during autumn, winter and spring, the mycelium is becoming more abundant, a stage is arrived at, usually about June, when the plants can no longer react (by forming more roots)

against the attack of the fungus, and then a zone of dead grass appears. Doubtless drought may assist in hastening on this stage, but I do not think it is the primary cause. Further, I have seen this advancing zone of infected grass dying down rapidly when the soil has been quite moist, and had been so for weeks previously.

The observation that fairy rings thrive best in dry seasons seems quite in accord with what might be expected, for mycelium in soil would bring about such a condition that the little rain that falls would not soak in and thus the vitality of the grass would be lowered and consequently conditions would be more favourable for the parasitic fungus. It seems quite possible that in dry seasons this zone might be so lacking in moisture that some plants would really die owing to drought.

I have mentioned(1) that in some years it is quite possible for the mycelium to grow outwards and only occasionally be present in the soil in sufficient quantity to kill the grass; I have seen cases where part of a ring may not die down at all one year and yet the ring as a whole may advance fairly uniformly. This has happened in an unusually damp year when the growth of the grass has been favoured by the moist weather conditions, as well as by the presence of certain decomposition products rendered available by the activity of the fungus mycelium present, and although some of the roots have succumbed to the toxic effect of the fungus, in this case the host has kept the upper hand, formed more roots and flourished.

Wet seasons must also act to the advantage of the grass and against the fungus because the toxins excreted by the fungus, being soluble, are continually draining away. In agreement with this but yet to a certain extent supporting the view that drought is the chief factor in bringing about the death of the grass is that, in the neighbourhood of Birmingham, fairy rings are far more common and show better development on sandy soils than on clay soils; but this observation also supports my view, for grass being more vigorous on clay soils, owing to clay being more retentive of moisture, is not likely to suffer so much from attacks of *M. oreades*.

Shanz and Piemeisel unfortunately do not give any details of microscopic examinations of *A. tabularis* rings beyond the abundance or otherwise of mycelium in the different zones of the ring. It would be interesting to know if any difference is distinguishable between the roots of grass in normal and in infected soil such as I have noted in connection with *M. oreades* rings.

That the effect of *M. oreades* on grass in Eastern Colorado should be so different from its effect in England and elsewhere is a matter of

surprise and interest. According to Shanz and Piemeisel, although it forms fairy rings, the only effect produced on the vegetation is to stimulate growth, a zone thus being produced, which may be compared to the outer stimulated zone of the ring of *A. tabularis*.

These authors report that only a small amount of mycelium is developed and that it is comparatively difficult to distinguish the threads in the soil; this is at variance with observations in England where a bare zone is formed and the mycelium is so abundant in the soil underneath this that it can be seen with the naked eye, and often before the dying down of the grass can be plucked like fragments of cotton wool from the surface of the soil.

Also, the production of the sporophores on the advancing edge of the stimulated zone, where the mycelium must be least abundant seems an unusual procedure, and different from the course of events in England, fruit bodies being produced where mycelium is most abundant.

In this stimulated area authors consider the fungus mycelium is reducing and living on the products of the organic matter in the soil: this may take place to a certain extent, but the parasitic action of the fungus destroying and decomposing the rootlets also accounts for some of the stimulation. If the stimulation were chiefly due to the reduction of the organic matter in the soil, surely when the advancing edge of a ring were treated with organic manure on which it is possible for the fungus to live saprophytically instead of the ring being destroyed the fungus would benefit. On the contrary, rings thus treated have disappeared, and when the rings were only treated with manure in patches, only the patches disappeared: grass flourished to the detriment of the fungus.

That the fungus can live as a pure saprophyte I have proved by growing the mycelium on various artificial media and on sterilised green grass.

Type II. The ring of *type II*, in which the grass is only stimulated, no damage apparently being done, is well illustrated in England by the *Tricholoma personatum* (Fr.), *T. nudum* (Bull.) and *T. panaeolum* (Fr.) rings.

Usually the sporophores of these rings appear during the autumn, but in 1923, on Ladbrooke Park (Warwickshire) golf course, a very perfect ring caused by *T. personatum* produced countless sporophores during January 10th to 23rd (the season was a mild one). In this case the presence of the fungus had been somewhat detrimental to the growth of the grass, for the grass of the fairway, after being cut in August 1922,

had grown well except on the actual ring (width 1½ to 2 ft., diameter of ring about 5 yards), where though very short it was conspicuous as regards its dark green colour. An examination of the soil under these *Tricholoma* rings reveals only a very small amount of mycelium, which does not cling about the roots of the living grass as the mycelium of the *M. oreades* does.

The fungus here is evidently not behaving as a parasite but living saprophytically on the humus and dead rootlets in the soil as it progresses: the stimulation generally seen being doubtless due to the products of decomposition rendered available to the grass by the fungus.

A pasture in which large rings of *T. panaeolum* appeared during the autumn of 1910 and of 1911 was heavily manured and a crop of grass taken off the following June. This treatment did not favour the growth of the fairy rings, for they never appeared again: the high nitrogenous manuring of the land by encouraging a vigorous growth of grass acted detrimentally to the further growth of the fungus.

T. personatum and *T. nudum* are met with in woods as well as in pastures growing saprophytically on dead leaves where they sometimes form fairy rings. Being edible, they are cultivated in France and elsewhere on beds of oak and other leaves, the acidity of such a bed being to a certain extent neutralised by adding a little stable manure.

Rings of *Lycoperdon gemmatum* (Batsch.) and *Agaricus arvensis* (Schoeff.) also belong to *type II*, and *Agaricus campestris* (Linn.) both in England and in Eastern Colorado conforms to this type.

Type III. Among rings of *type III*—those which do not affect grass—may be counted *Hebeloma crustuliniforma* var. *minor* (Bull.) and *Tricholoma sordidum* (Fr.). A very perfect ring of the former, 38 in. diameter, appeared on my lawn in August 1922 but never reappeared. The ring did not affect the grass at all. Abundance of mycelium was visible just around the base of the sporophores mixed up with dead rootlets and moss, but the ordinary sod underneath the ring did not show more mycelium than is usual everywhere in turf, in fact was quite normal.

Two rings of *T. sordidum* appeared on the same lawn in 1921 and lasted three years. An examination of the turf showed that the fungus was living saprophytically at and very near the surface of the ground. There were indications that the fungus lived on dead moss and dead root hairs of grass.

These rings, which were only about 22 in. inner diameter when first noticed and from 6 to 12 in. wide in the ring area, progressed from 12 to

18 in. during the second year. During the third year, instead of having the grass cut, it was allowed to grow in order to observe the effect on the fungus; only a few sporophores appeared and in 1924 there was no trace of the ring; it may have been that grass living normally under good cultural conditions instead of being continually cropped excreted something toxic to the fungus.

Chemical Changes produced in Soil.

Concerning the chemical changes produced in soil during the progress of fairy-ring fungi very little work has been done.

Lawes, Gilbert and Warrington (1883)(2), and Molliard (1910)(4), investigated some of the chemical changes occurring in connection with *M. oreades* rings, while Shanz and Piemeisel (1917) give some details of a chemical investigation of the rings formed by *A. tabularis* (Pk.) and *C. cyathiformis* (Bosc.). Lawes, Gilbert and Warrington investigated fairy rings in order to determine the source of the nitrogen of the fungi, which apparently were the cause of a natural rotation of crops. They found that there was more nitrogen outside the ring, in the ordinary sod, than on the ring or inside, but that nitrates were far more abundant on the ring and they concluded that the source of the nitrates was the organic matter of the soil.

Molliard(4) concluded that the mycelium acted directly on the organic matter of the soil, giving rise to ammoniacal salts; he found most ammonia under the dead grass zone and noted very little difference between the amount present outside and inside the ring.

As regards the ammonia content Shanz and Piemeisel agree with Molliard that most is to be found in the ring area, but less without than within the ring. With regard to nitrates the figures of Shanz and Piemeisel seem rather too variable to draw conclusions from, but these authors summarise by saying that ammonia is more abundant in the soil well permeated with mycelium, whereas nitrates are more prevalent in the part occupied by the old dying mycelium.

Now when determining the *total* nitrogen (in any form) both Lawes, Gilbert and Warrington, and Shanz and Piemeisel, found more outside the ring in the ordinary soil than on it, and concluded that the source of the nitrogen bringing about the stimulation of growth of fairy rings is the organic matter of the soil, which, owing to the activities of the fungus mycelium, gives up its nitrogen in a form such as ammonia and nitrates which can be easily assimilated by grass, hence that nitrogen is only changed from one form to another.

Through the kindness of Professor Ling and Mr A. Brookes of the Biochemical Department of the Birmingham University, I obtained the following determination of the nitrate and ammonia content of samples of soil taken from three different zones of a fairy ring (*M. oreades*)[1] and from the normal soil outside it.

	Total nitrogenous matter %	Ammonia salts and free ammonia %	Nitrates and nitrites	Moisture %
Inner stimulated zone (*a*)	0·243	0·00375	Nil	16·25
Dead zone (*b*)	0·253	0·00326	,,	18·84
Outer stimulated zone (*c*)	0·204	0·00196	,,	20·10
General field	0·218	0·00117	,,	20·76

The soil samples were taken by boring to a depth of about 12 in. with a sharpened gas pipe (inner diameter 1 in.). Three borings were taken from each zone and from the surrounding field. The soil from the ring had a particularly offensive smell, especially in the dead zone. The total nitrogenous matter (not including nitrates and nitrites) was estimated by the method of Ling and Price(3). The ammonia salts and free NH_3 were determined by shaking the soil with distilled water and distilling the extract with 40 per cent. soda and nesslerising as in the microkjeldahl method. In determining the nitrates and nitrites the extract used for the ammonia salts and free ammonia was employed. The salts were reduced by means of aluminium amalgam, distilled with 40 per cent. soda and nesslerised as before: the results give the total nitrogen in the following forms: ammonia salts, free ammonia, nitrates and nitrites. In order to determine the nitrates and nitrites the percentage of ammonium salts and free ammonia is deducted from the percentage of total nitrogen.

The results in columns 4 and 5, *i.e.* the finding of no oxygenated derivatives of nitrogen, and the high moisture content, seem rather unusual, but the samples were taken in August 1922, after there had been heavy rains for several weeks and the ground was thoroughly soaked, so that any nitrates probably drained away in solution as quickly as formed. Samples taken in July from the same ring gave the usual results as regards moisture:

Inner stimulated zone	8·82	per cent.	water
Dead zone	5·74	,,	,,
Outer stimulated zone	5·79	,,	,,
General field	12·76	,,	,,

[1] Only a small portion of this ring and very few sporophores appeared in 1923, and no trace of it was seen in either 1924 or 1925.

It will be noted that the ammonia content is highest in the area of the inner stimulated zone and is very nearly the same under the dead zone; judging from the figures given by Molliard, and Shanz and Piemeisel, the ammonia content is usually highest under the dead zone, but the tables of Shanz and Piemeisel show instances parallel with the above: perhaps this may be correlated with the finding of no nitrates in the inner stimulated zone, which is usually the zone associated with an abundance of nitrates, bacterial action there usually changing the ammonia salts formed in the previous year into nitrates. But it is rather remarkable that the outer stimulated zone should have less nitrogen taken as a whole than is to be found in the field generally: perhaps this may be due to the fact that the outer stimulated area is producing a good crop of grass and so uses more nitrogen compared with that used in producing the normal poor crop of the field.

It will also be noted that the dead zone and inner stimulated zone have gained nitrogen, since the total amount of nitrogen outside the ring is less than in these zones; this does not agree with Lawes, Gilbert and Warrington's results or with most of the results of Shanz and Piemeisel.

Although the results of Lawes, Gilbert and Warrington and of Shanz and Piemeisel point to the conclusion that there is no fixation of nitrogen by fairy-ring fungi, but only a change of the nitrogen into a more easily assimilable form, it seems desirable that culture experiments should be made in order to settle this point. The mycelium of *M. oreades* and other fairy-ring fungi can easily be grown on artificial media so that the problem should not be a difficult one for a chemist.

In conclusion I would add that I consider a fairy-ring fungus such as *Marasmius oreades* (in England) behaves as a parasite and in its progress destroys grass by some toxic excretion, and the fungus lives saprophytically on the dead organic matter thus produced and on any other already present in the soil. The grass which appears on this dead zone the year following the destruction, owes its luxuriance to the easily assimilable nitrogenous compounds resulting from the activities of the fungus mycelium, in its destruction of the grass, and also to similar compounds produced by the decay of the mycelium itself. Further, during several months of the previous year this zone did not support a crop, and the soil here, in dry years especially, does not suffer the usual loss from the draining away of soluble food substance.

SUMMARY.

1. Observations are made on the growth of three types of fairy rings found in pastures and elsewhere.

2. *Marasmius oreades* belongs to a type which causes the death of rings of grass. It behaves as a parasite, destroying grass by means of a toxin.

3. Comments are made on the views of Shanz and Piemeisel, who consider the death of the grass in certain fairy rings is merely due to a drought produced by the presence of mycelium in soil.

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NOTE ON THE OCCURRENCE OF DISEASED SHOOTS ARISING FROM POTATO-TUBERS INFECTED BY *PHYTOPHTHORA INFESTANS*

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(With Plate V.)

For more than 60 years the problem of the perpetuation of the potato-blight fungus (*Phytophthora infestans*) from year to year has exercised the minds of mycologists. By analogy with the life-history of closely related fungi, two methods of hibernation have been considered possible: (1) the fungus may exist in the form of oospores which on germination the following year attack the potato plant and cause the first outbreak of disease for that season; or (2) the fungus may hibernate in the form of mycelium within the potato tuber and grow out into a new shoot and there produce spores. So far, however, oospores have never been found in the living or dead tissues of the potato plant, and their production has only been observed when the fungus has been cultivated artificially on a certain nutrient medium.

Supporters of the theory that the formation of oospores must take place in nature and that this is the normal, common method of the perpetuation of the disease from year to year point out, as justifying their belief, the fact that experiments proving that the disease can arise each season on shoots produced from infected seed tubers have been very few in number—the authentic cases being apparently but four. We have now to record a fifth case—the first observed in this country. Before giving the details of our experiments, we will review briefly and critically, the work, relevant to the present subject, of the previous investigators, viz. de Bary, Jensen, Dr Pethybridge and Prof. Melhus.

De Bary's experiments were of two kinds: (1) in 1861 with naturally infected potato-tubers, grown either in the house or in the laboratory; and (2) in 1875 with artificially infected tubers, planted in a garden.

De Bary's earlier observations(1), which are unaccompanied by any